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Effects of training on memory-guided saccade performance

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Abstract

Sensory–motor transformations are often studied using memory-guided movements to small numbers of targets. Whether target locations are directly converted into motor plans on every trial, or subjects use targets to select one of a small number of previously memorized trajectories is unknown. Well-trained monkeys made memory-guided saccades to familiar or nearby novel targets. Performance was superficially similar under the two conditions. However, saccades to novel targets close to the vertical meridian were repulsed away from the nearest familiar target. These findings suggest that sensory-to-motor transformations are performed on every trial, but that previous experience may bias the transformation.

JEL classification: *Macaca mulatta*
Keywords: Categorical perception; Visual memory; Saccades; Monkey

1. Introduction

In order to study how the brain performs sensory to motor transformations, animals are often trained to respond to specific sensory stimuli, which are presented to them over and over again. Does the repetitive presentation of a small number of targets change the animals' performance? Consider a simple remembered saccade task, in which animals are trained to memorize the location of one target and move the eyes toward it after a memory interval. It is conceivable that, when trained on a relatively small number of targets, all possible movement trajectories or movement endpoints are memorized, and that the target location merely serves as a cue to identify which of these should be retrieved from long-term storage and performed. Alternatively, there could be a true sensory to motor transformation on every trial, in which the spatial location of the target is directly converted into a motor plan.

Many psychophysical, imaging and neural recording experiments use delayed saccade paradigms to study sensory–motor transformations. If subjects treat overlearned stimuli differently than novel stimuli, we could not generalize from these experiments to routine behavior.

We set up our experiment to distinguish among three possible strategies. Subjects could directly convert the location of a target into a motor command, which would then be executed. With this strategy, saccades should land as close to novel targets as to familiar targets. Alternately, subjects could memorize each of the small number of possible trajectories or endpoints and use the stimulus location to select one of these memorized trajectories or endpoints. If subjects used this strategy, saccades to novel targets should be directed not toward the actual location of the novel target, but instead to the location of the closest familiar target.

A third strategy could involve coding novel stimulus locations with respect to familiar locations. The use of this strategy could result in saccades to novel stimuli being biased by the location of the familiar target. For example, subjects using this strategy might report saccades as being repulsed away from the location of the familiar target. Evidence for such an effect has been reported for experiments on human subjects. Stimuli falling near but not on a category boundary (such as an imagined vertical line separating the left and right sides of a circle) result in subjects reporting a location that is biased away from the boundary (Gourtzelidis, Smyrnis, Evdokimidis, & Balogh, 2001; Huttenlocher, Hedges, &

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Duncan, 1991; Sandberg, Huttenlocher, & Newcombe, 1996). If subjects treat familiar locations as boundaries (that is, categorize novel stimuli as clockwise or counterclockwise from a familiar location), we might expect to find a similar repulsion effect for novel stimulus locations very near to, but discernibly different from, the familiar stimulus locations.

2. Methods

In order to determine whether memory-guided saccades were affected by target familiarity, we overtrained five rhesus macaques on a center-out memory-guided saccade task to five different target locations (Fig. 1). Monkeys memorized the spatial location of a flash of light, and later made a saccade to that position. Once proficient (>95% success rate), we recorded the endpoints of saccades made to familiar and unfamiliar target locations.

2.1. Apparatus and surgical procedures

Each monkey was fitted with a head-holder and scleral search coil in an initial sterile surgical procedure. All procedures were in accordance with NIH guidelines and were reviewed by the Washington University IUCUC. Monkeys sat in a custom box (Crist Instruments) with their heads restrained by a head post. Eye position was recorded every 2 ms with 0.03° resolution (CNC Inc.). For four animals, stimuli were back projected onto an otherwise black screen in a completely dark room using an Electrohome projector. For monkey H, stimuli were presented on a video monitor whose background was dimly illuminated and therefore formed a visible frame around the stimulus display.

2.2. Subjects

Three monkeys were previously overtrained on center-out memory-guided eye (monkeys D and E) or eye and arm (monkey I) tasks, using eight target locations and a memory period of up to 1.6 s. Each animal had at least two years of practice on this task prior to the start of these experiments. For the current experiments, we used just five of the eight previously overtrained locations. These three animals had been used in neural recording experiments and had recording chambers located over the intraparietal sulcus. In order to rule out artifacts due to previous training and/or electrode penetrations, we tested two additional monkeys (J, H) that were completely naive prior to the start of this study. They had never performed eye movement tasks, center-out tasks or memory tasks, and had not been involved in neural recording experiments.

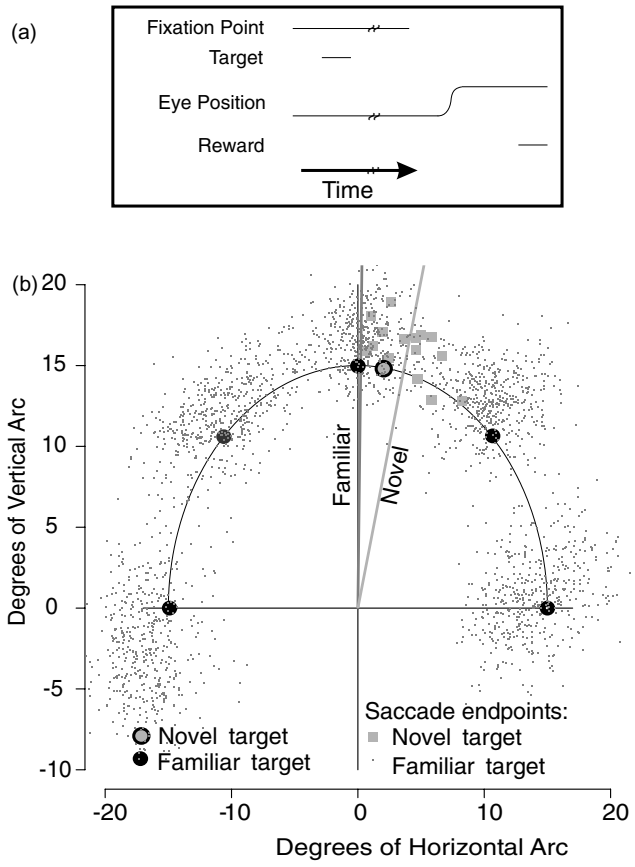

Fig. 1. The center-out delayed saccade task. (a) Trials began with a fixation point at the center of the screen. A 150 ms flash (target) was presented in the periphery at one of five familiar locations. Subjects were required to maintain fixation on the fixation point until it disappeared after a variable memory interval. After the fixation point disappeared, the animal had 500 ms to make a saccade to within 10° of the remembered location of the peripheral flash. When eye position had been held for 350 ms at the correct location, monkeys were rewarded with a drop of water or juice. (b) Target locations and saccade endpoints. Horizontal and vertical lines represent horizontal and vertical meridians of the subject's visual field. Black circles represent the locations of five familiar targets for monkey E. Small gray points represent saccade endpoints for monkey E. The large gray circle represents the location of a novel target, presented about once every 40 trials. Large gray squares represent the saccade endpoints for all trials in which this novel target was presented. On average, saccades to the novel target (mean direction indicated by the gray radial line marked 'novel') were displaced to the right of the actual target location, while the direction of saccades to the closest familiar target were very accurate (mean direction indicated by the gray radial line marked 'familiar').

2.3. Procedure

Monkeys performed a memory-guided center-out saccade task (Fig. 1a). A trial began with fixation of a dot near the center of the screen. A short target flash (150 ms) was presented in the periphery at one of five familiar locations. Each subject was required to maintain fixation (within 4°) on the center dot until it disappeared. The memory interval was variable, and

Table 1
Performance of five monkeys on memory-guided saccades to familiar and novel targets

Monkey	Familiar saccades		Novel saccades		Novel saccade frequency (%)	Memory period errors (%)
	Number	Error rate (%)	Number	Error rate (%)		
D	8075	3.5	792	0.8	8.9	10.8
E	2400	2.8	270	0.7	10.1	12.5
I	2712	2.2	412	2.6	13.2	5.8
J	14002	3.3	539	4.4	3.7	18.5
H	5042	3.7	373	1.8	6.9	18.6

The novel saccade frequency was calculated as the percentage of total trials. Trials in which the animal left the fixation window prior to the end of the memory period ('memory period errors') and excluded from all but the last column.

ranged from 1.1 to 1.9 s in monkey H to 3.0–3.6 s in monkeys D and E, with increments of 0.1 s. After the center dot disappeared, the animal had 500 ms to make a saccade to within 10° of the remembered location of the peripheral flash, and was required to hold that location for 350 ms.

Correct trials were rewarded by drops of water or juice. Correct trials were those in which the eyes remained within 10° of the target for 350 ms. Acquisition errors occurred when fixation was held until the fixation spot was extinguished, but the saccade landed more than 10° from the target, or a second movement within 350 ms carried the gaze outside this window. During off-line data analysis, trials ending in acquisition errors were treated the same as correct trials (see below). Memory period errors occurred when fixation was broken before the fixation spot was extinguished. Memory period errors resulted in a short time out. Trials ending in memory period errors were tallied but saccade endpoints were excluded from further analysis. In order to encourage accurate behavior, a double reward was delivered on correct trials when the animal landed within 6° of the target (except for monkey J, who received at most one reward per trial). A single reward was delivered if the animal landed between 6° and 10° of the target. For animals D and E, saccades landing within 8° of a novel target (see below) were doubly rewarded; for animals H and I, double rewards were restricted to familiar target trials. Note that the reward schedule was slightly biased towards novel targets for animals D and E, towards familiar targets for H and I, and was neutral for J.

Monkeys D, E and I were overtrained on memory-guided saccades to each of five peripheral target locations, all of which were 15° (D and E) or 20° (I) from the fovea. Targets were evenly spaced in a circular arc from directly to the right (0°), diagonally up and to the right (45°), straight up (90°), up and to the left (135°) or directly to the left (180°). Fig. 1b shows locations of the familiar targets relative to the central fixation dot. The small gray dots represent saccade endpoints for monkey E.

Monkeys H and J were overtrained on targets that were shifted by 8° counterclockwise from those of the other animals; that is, they were located at −8°, 37°, 82°, 127° and 172°. The rationale for this shift will be discussed below. Target eccentricity was 16°.

Animals were trained until they completed successfully at least 95% of the trials they began. This required ~30 sessions of 250–750 trials each for the two naïve animals, and 7–12 sessions of 500–2000 trials each for the three experienced animals. At this time, data collection was initiated. The same five familiar stimuli were presented, but additional novel targets were added infrequently. These novel targets were placed 2°, 4°, 8°, or 16° of arc away from a familiar location in either the clockwise or counterclockwise direction, at the same eccentricity as the familiar target. In three animals, novel targets were also presented 1° away. The location of one novel target 8° clockwise from the vertical target is shown in Fig. 1b for monkey E. The large gray squares represent saccade endpoints for trials where this was the target.

The relative frequency of all novel targets compared to all familiar targets is listed in the second to last column of Table 1. In any one experiment, all five familiar targets were used, and novel targets were placed around only one of these familiar targets. Data for each experiment were collected in three to six sessions. A total of 11 experiments were conducted.

2.4. Data analysis

In initial pilot experiments, we determined that the variable (non-systematic) error associated with memory-guided saccades was minimized when we considered only the eye position at the end of the saccade (absolute saccade endpoint). Variable error was similar or larger when we instead considered the actual saccade trajectory (ending position minus starting position, a relative measure of saccade endpoint). Variable error was also larger when we considered the difference between eye position at the time of target appearance and eye position at the end of the saccade (a second relative measure of saccade endpoint). This suggests that the animal used the fixation point, which was visible at the time of target appearance and remained visible until shortly before the

Table 2
Best fit coefficients for the deviations of memory-guided saccade endpoints away from novel targets located close to familiar targets

Familiar target location	Monkey	H coefficient	P value for H coefficient	P value for W coefficient
Horizontal (right or left)	J	2.1	0.15	0.20
	H	−1.1	0.44	0.52
	D	−1.8	0.61	0.62
Diagonal (up right)	E	2.7	0.32	0.37
	I	−3.5	0.04*	0.18
	J	3.2	0.09	0.16
Up (90°)	D	12.9	0.0000*	0.0000*
(90°)	E	4.4	0.17	0.13
(90°)	I	5.0	0.0001*	0.0000*
(82°)	J	3.3	0.0001*	0.0002*
(82°)	H	3.7	0.0001*	0.0006*

The H coefficient (2nd column) is proportional to the amplitude of any systemic deviation. Positive values indicate a repulsive bias away from the nearby familiar target and negative values indicate an attractive bias. Significance of the fit is indicated by the P values assigned to the H and W coefficients (3rd and 4th columns, respectively). Significant effects (either repulsive or attractive) are indicated by "*" ($P < 0.05$). See text for additional details.

saccade, as a landmark to help locate the (absolute) location of the target. We therefore have used absolute saccade endpoint for most of the remaining analysis. However, we repeated the critical analysis illustrated in Table 2 (see Section 3) using relative rather than absolute saccade endpoint and confirmed that this did not affect our overall results.

Guided by our pilot study, we calculated the mean saccade direction for each target, treating the fixation spot as the origin. Saccade direction was defined as the arc tangent of the ratio of vertical to horizontal eye position, obtained in the interval from 50 to 250 ms after the end of the first saccade following fixation spot offset. Both trials classified as successful and trials classified as acquisition errors were analyzed. However, saccades of less than 8° in amplitude (0.87% of all saccades) and saccades which landed more than 20° from the target (0.15% of all saccades) were eliminated. Saccades were identified automatically as a change of at least 4° in the low-pass filtered horizontal or vertical eye position. The start of the saccade was then identified by looking backward in time until both horizontal and vertical eye velocity dropped below 30°/s; the end of the saccade was identified by looking forward in time until both horizontal and vertical eye position dropped below 24°/s.

Next, we asked how saccades to novel targets were influenced by neighboring familiar target locations. Our null hypothesis was that saccades to novel and familiar target locations would be similar to one another. In order to test this hypothesis, we could not directly compare the endpoints of the two types of saccades, since their targets would not be at the same location. Furthermore, we could not compare the endpoints of memory-guided saccades to novel targets with the target locations themselves, since it is clear from many studies that memory-guided saccades do not land exactly on target, due to vertical upshifts and idiosyncratic biases (Stanford & Sparks, 1994). Instead, we compared the direction of saccades to novel targets against an expected direction. Expected direction (E) was calculated as a linear interpolation between the direction of saccades to familiar targets (μ_F) and the direction of saccades to novel targets sufficiently far away from the familiar target (16°) so as to be minimally affected (μ_{16}):

$$E = \mu_F + \frac{(\mu_{16} - \mu_F)}{16} \times (N - F)$$

where N = novel target direction and F = familiar target direction.

Directional errors were computed by subtracting the saccade direction from this expected direction. For a saccade to a novel target 8° from a familiar target, for example, the error was calculated as the distance of that saccade's endpoint to a point midway between the mean endpoints of saccades to the familiar target and saccades to the 16° target. As a result of this transformation, memory-guided saccades are associated with an error, which is a difference between the actual and the expected saccade direction. By definition, saccades to familiar locations will always have an error of zero. If our null hypothesis is correct (saccades to novel and familiar targets are treated similarly), then saccades to novel target locations will also have zero error. It is important to understand that "zero error" means that the saccade lands exactly on the *predicted* target location, not on the *actual* target location.

Consider the following example. A saccade to a familiar target lands two degrees to the right of the intended target. The saccades to targets at ±16° also land two degrees to the right of their targets. Now a novel target is presented, close to the central familiar target. Imagine first that the null hypothesis is correct. In this case, the novel saccade will land two degrees to the right of the intended target. After the transformation, the

saccade has an error of zero—it lands exactly on the predicted target location. We will refer to this as landing "on target", even though the saccade has landed two degrees to the right of the actual target.

Now imagine that the null hypothesis is false, and that the saccade to the novel target lands one degree to the right of the intended target. After the transformation, this saccade has an error of −1°—it has landed one degree to the left of where we expected it to land, based on the null hypothesis. We will refer to this as landing one degree to the left of the target, even though the saccade has in fact landed to the *right* of the actual target. We take this liberty in terminology because our null hypothesis is not that memory-guided saccades to novel targets will land exactly on target, but instead, that they will be subject to the same ideosyncratic biases that saccades to familiar targets are subject to, and it is the deviation from the predictions of this null hypothesis that we wish to emphasize.

If saccades towards novel targets are biased towards the closest familiar target, then a saccade to a target in a clockwise direction from a novel target (the negative direction, by convention) will result in a counterclockwise (positive) error. In general, an attractive bias will be indicated by an error with a sign opposite to the deviation of the novel target, while a repulsive bias will be indicated by an error with the same sign.

In order to obtain a quantitative measurement of the degree of repulsion or attraction from familiar locations, we plotted directional error as a function of target location, relative to a familiar target, and then fit the error data to a Gabor function: $H \times e^{(W \times x)^2} \sin(W \times x)$. Examples of fits to this function are shown in the gray lines of Figs. 2 and 3. X is the angle of a target away from a familiar location and H and W are coefficients determined by the data. This function is zero at $x = 0$, corresponding to the fact that saccades towards the familiar target will by definition have no error. The function also tends towards zero as x gets very positive or very negative, corresponding to the fact that the influence of a familiar target will drop towards zero as the novel target is placed farther and farther away. The coefficient H is related to the amplitude (height) of the function, which corresponds to the degree of attractive or repulsive bias. An H coefficient that is not significantly different from zero indicates no bias. A negative value of H indicates an attractive bias, while a positive value indicates repulsion. The parameter W describes how far from the familiar location the effect persists. W is inversely related to the spatial spread (width) of the function.

Fits, including statistical significance, were determined using non-linear least squares estimation (Bates & Watts, 1998) and constrained to be symmetric and therefore to be zero at the familiar target. Analyses were performed using the *R* statistical package (http://www.r-project.org).

3. Results

All five animals performed the task well. On 81–94% of trials, fixation was maintained for the duration of the memory period (Memory period errors, Table 1). For these trials, animals successfully brought their eyes to within 10° of the original target location on 96.4–97.8% of trials. Error rates associated with novel targets are no higher than those associated with familiar targets (Table 1). Only one animal had a higher error rate in novel than familiar trials, and even in that one animal, the difference was not significant (monkey J, Pearson's chi-squared test, $P = 0.22$). Surprisingly, monkeys D and E showed significantly *lower* error rates in novel compared to familiar trials (Pearson's chi-squared test, $P < 0.05$). Possibly animals were alerted by the novel target locations, and as a result were less likely to make an error.

For the most part, saccades made to novel target locations were similar to saccades made to familiar target locations. Fig. 2 shows the deviation of the endpoints of saccades to eight novel targets, centered about a familiar target located on the right and 8° below the horizontal meridian (monkey H). The horizontal axis shows the polar angle of each target, and the vertical axis shows the angular difference between the actual and expected saccade endpoints. The saccades directed to the central (−8°) familiar target, as well as saccades directed to targets ±16° away from the familiar target, provide the standards against which to compare the saccades

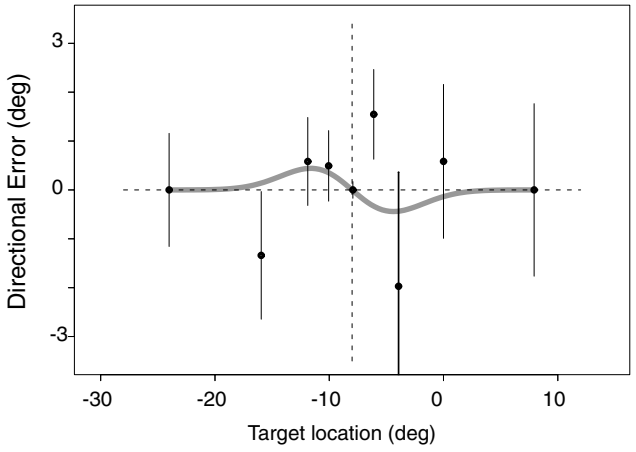

Fig. 2. Mean errors in saccade direction to novel targets close to the horizontal meridian. Vertical dotted line designates the familiar location (−8°). Saccades to this target and to targets 16° to either side (−24° and +8°) serve as control saccades and therefore are plotted as having zero directional error. Circles show the mean directional error for the endpoint of saccades to novel targets ±2°, 4°, 8° and 16° from the familiar target, and bars represent standard errors. The gray line is the best fit Gabor function to the data. See Table 2 for significance and values for all directions for all monkeys. The fit is not significantly different from a flat line, indicating that saccades to novel targets close to the horizontal meridian were biased neither towards nor away from a nearby familiar target. Data are from monkey E.

directed to novel targets. These three standard saccades (to targets at −24°, −8° and +8°) are therefore plotted as having zero directional error. The remaining data points show the directions of saccades to novel targets, relative to an expectation based on the three standard targets (see Section 2). Saccades to novel targets are deviated from their expected endpoints by up to 2°. However, there is no consistent pattern to these deviations, and in all but one case the mean endpoint differs from zero by less than one standard error of the mean. The fit of the Gabor function to these data was not significant ($P = 0.45$, Table 2), indicating no significant effect of the familiar target on saccades to nearby novel targets.

Table 2 shows data from all 11 experiments in which infrequent novel targets were placed close to a familiar target. The experiments are grouped by the location of the familiar target about which the novel targets were placed. Novel targets located to the right, to the left, or diagonally up and to the right of the fovea were not associated with biased memory-guided saccades. In three of six experiments, a negative H coefficient was obtained, consistent with an attraction of saccades towards a nearby familiar location. However, in the other three experiments a positive H value was obtained, consistent with a repulsion. These coefficients were statistically significant in only one of six conditions, and in that condition (monkey I, target diagonally up and to the right), the fit of the second coefficient was not significant. Thus, for three out of four locations tested, memory-guided saccades to novel targets were not influenced by proximity to a familiar target.

The results were markedly different for novel targets near a familiar target located within 8° of straight up, however. Here, errors were systematically in the same direction as the novel target (clockwise targets resulted in clockwise errors.) In all five cases a positive H coefficient was obtained, and every coefficient was larger than the largest coefficient obtained at any of the other three locations (0°, 45° or 180°). In four out five of these cases, the fits were highly significant. This indicates that, for targets directly above the fovea, memory-guided saccades directed towards a novel location that lies close to a familiar location are biased away from that familiar location. Thus, a near-vertical memory-guided saccade to a novel target located near a familiar target location does not land, on average, at the novel location, nor at the familiar location, nor somewhere in between. Instead, if a novel target lies clockwise from a familiar

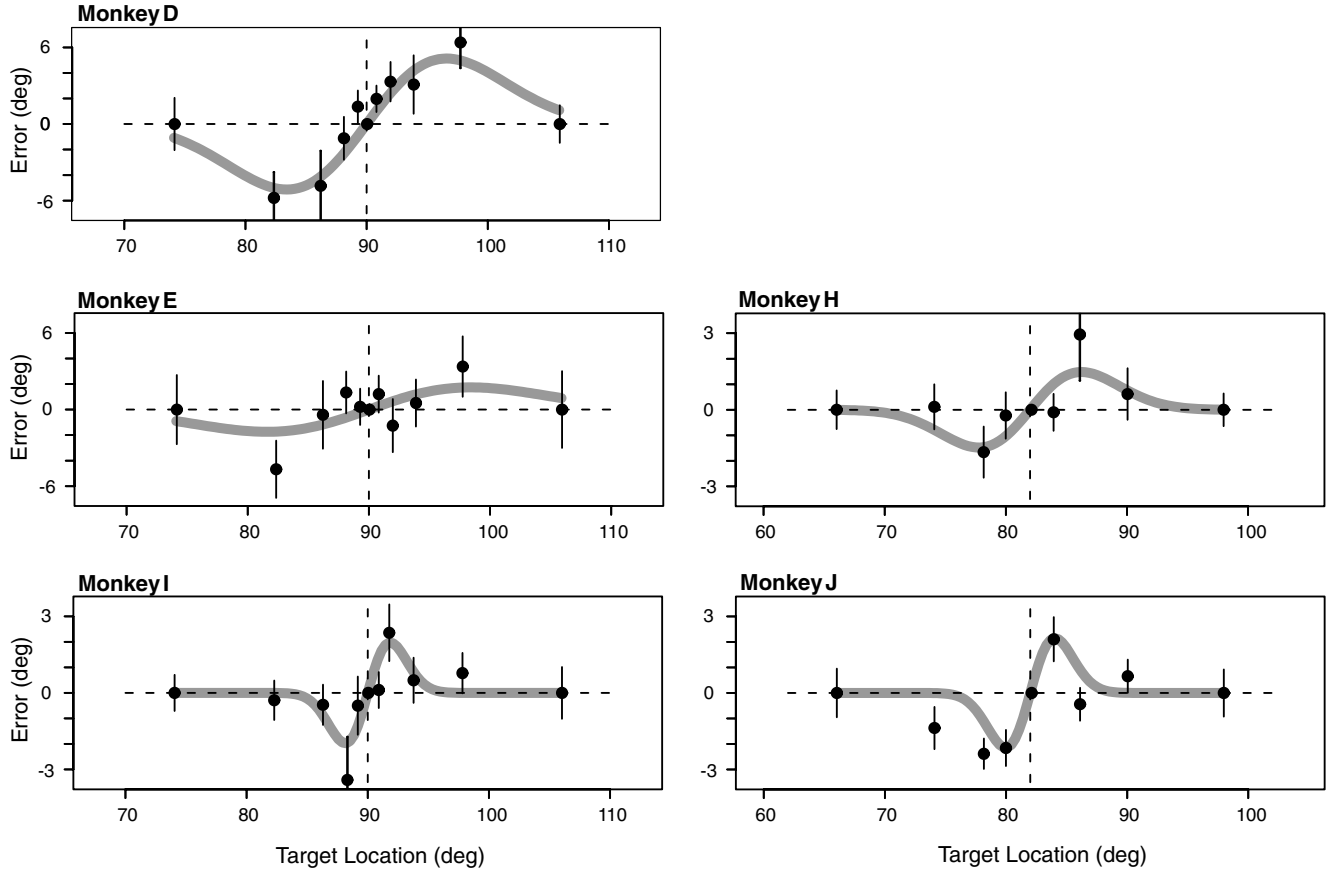

Fig. 3. Mean errors in saccade direction to novel targets close to the vertical meridian. Same format as in Fig. 2. Data shown for all monkeys. See Table 2 for significance of fit to Gabor function. The Gabor fits (gray lines) are significantly different from flat lines for all but monkey E, and indicate that saccades to novel targets close to the vertical meridian were biased away from nearby familiar targets.

location, the monkey reports it as lying even further clockwise than its true position. Fig. 1b shows this for one novel target near the vertical meridian for monkey E. Note that, for the illustrated novel target (gray circle near the vertical meridian), saccades are, on average (gray radial line marked 'Novel'), repulsed away from the nearest familiar target (gray radial line marked 'Familiar').

Fig. 3 shows the data and best fit Gabor function for all the data from all five animals. Consider the data of monkey D. Instead of landing on the expected target locations (dashed horizontal line), saccades were consistently biased away from the novel targets. The strongest effect (mean deviation, indicated by distance along the *y*-axis) occurred with novel targets ±8° from the familiar target. The closest familiar target lay at 90° (vertical dashed line). Saccades to targets 8° clockwise of the familiar target landed, on average, 14° clockwise, while saccades to targets 8° counterclockwise of the familiar target landed 14° counterclockwise. Therefore, in each case the angle of these saccades exceeded or overshot the angle of the novel target, on average, by 6°. Symmetric repulsion can also be seen for targets at 1°, 2° and 4° from the familiar location.

The fit of the Gabor function to the data is remarkable, despite using only two free parameters. There were 13–70 individual data points per novel target location. The width and amplitude of the function were determined by the data.

There was surprising consistency across animals, despite some monkey-specific features. All data sets around familiar vertical targets show clear and symmetric repulsion from the familiar target location, indicated by positive deviations to the right of the center and negative deviations to the left. Peak effects occur at 8° (2 animals), 4° (1 animal) or 2° (2 animals) from the familiar location. In each case, the location of the peak is identical or nearly identical for targets on the right and on the left. Three animals show a "dead zone" immediately around the familiar target, in which saccades appear to be unbiased (E, I and H). A Gabor function has no such dead zone, and therefore the fits do not reflect this aspect of the data. The dead zone is particularly large (±4°) in monkey E and probably accounts for the failure of the fit to reach significance. Of the remaining two animals, one (D) is ambiguous with respect to a dead zone. The final animal (J) shows no indication of a dead zone, but the fact that data were not obtained at ±1° leaves the possibility open.

We repeated this analysis using relative saccade direction (eye position at the end of the saccade minus eye position at the start of the saccade; see Section 2). The results were very similar. The only notable change was in the repulsion effect from monkey J during near-vertical saccades, which failed to reach significance despite an H coefficient of 9.5. There were no other changes in the pattern of significant and non-significant effects. We also repeated the analysis using only those trials in which the starting point for the saccade lay within 2° of the fixation point, and the same pattern of results was obtained.

So far we have shown that memory-guided saccades directed towards targets near the vertical meridian show a clear and consistent repulsion effect. We have asserted that saccades are repulsed from familiar target locations that lie near the vertical meridian, but a simpler explanation is that saccades are simply repulsed from the meridian itself. In this case, then familiarity with the target location is irrelevant.

In order to determine whether repulsion is away from familiar targets or away from the meridian, we devised the following experiment. Two completely naïve animals (J and H) were trained to make remembered saccades to targets located 8° to the right of the vertical meridian (82° targets). Our logic was as follows (Fig. 4). A novel target 4° to the right of the meridian (86° target) would be located exactly between the meridian and the familiar target location. If the repulsion is away from the meridian and unrelated to past experience, then saccades to the 86° target should deviate away from the meridian and *towards* the familiar target. If instead the repulsion is away from a familiar target close to the meridian, then saccades to the 86° target should deviate towards the meridian and *away* from the familiar target.

The data from these two animals (J and H) appear in Table 2 and Fig. 3. In both animals, saccades directed towards the 86° target were clearly repulsed away from the familiar target location and towards the vertical meridian. This indicates that the repulsion is away from a familiar target, not away from the vertical meridian.

An even simpler test of whether saccades to near-vertical targets are repulsed away from the meridian, independent of target familiarity, is to check whether the saccades to the familiar 82° targets were themselves deviated away from the meridian. This was not the case. In both animals J and H, saccades towards the 82° target were not deviated away from the meridian; they landed on average at 83.5° and 82.5°, respectively. In other words, saccades to these familiar targets were if anything attracted towards the meridian rather than repulsed away from it. (This cannot be seen from Fig. 3, since these plots are arranged so that the deviation from the familiar target is equal to zero; see Section 2.)

Might repulsion have been from the apparent vertical, rather than from the true vertical meridian? This possibility can be ruled out by the data from animal H, who was shown familiar and novel targets within a rectangular frame whose edges were aligned with earth-horizontal and earth-vertical. This frame provided a veridical vertical reference, such that the 82° target would not be perceived as lying directly above the fixation point. From Table 2 it is evident that monkeys J

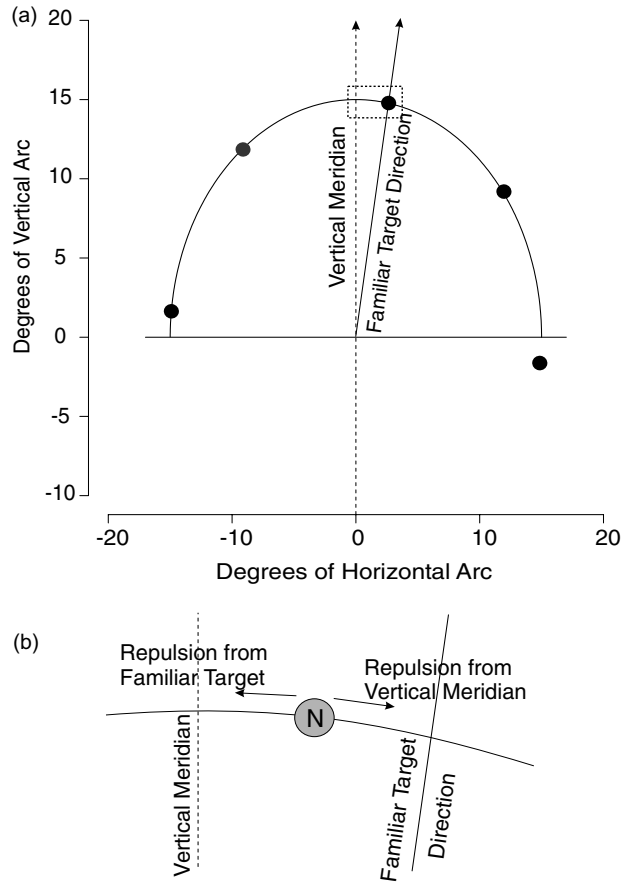

Fig. 4. Cartoon of logic behind −8° rotation experiment (Fig. 3, animals H and J). (a) Familiar target locations. Format as in Fig. 1b. (b) Magnification of dotted box from part a. Gray circle (*N*) represents a novel target 4° from the vertical meridian, halfway between the familiar target and the vertical meridian. If the repulsion effect is referenced to the vertical meridian, saccades to the novel target at 4° should be repulsed away from the vertical meridian, that is, to the right in the figure. On the other hand, if the repulsion effect is referenced to the closest familiar target, then saccades to the novel target should be displaced towards the vertical meridian (and away from the familiar target), that is, to the left. Fig. 3 (H and J) shows that saccades to novel targets at 86° were displaced towards the vertical meridian, indicating that the repulsion was referenced to the closest familiar target and not to the vertical meridian.

and H showed less repulsion than monkeys D, E and I. This could be a consequence of locating the familiar target 8° from the meridian instead of exactly on the meridian. However, there is another possible explanation. Animals D, E and I had years of experience with the familiar target location on the meridian. Animals J and H had only a month or two of experience. The idea that the repulsion effect may continue to increase with practice over the course of many months is supported by data from monkey J. This animal was first tested using novel targets close to the 82° target (four sessions). At this time, an H coefficient of 2.1 was obtained ($P = 0.08$). Over the subsequent nine sessions, novel targets near 37° and novel targets near −8° were tested. During these sessions, familiar targets continued to be presented, and the animal completed an additional 1904 saccades directed towards the 82° target. After the completion of these nine sessions, novel targets close to 82° were retested (four sessions), and this time an H coefficient of 5.4 was obtained ($P = 0.0004$). Thus, over the course of nine sessions, the repulsion effect more than doubled. We conclude that the relatively small amount of experience these two animals had with the familiar targets accounts at least in part for the relatively small repulsion effect observed.

We expected that variability would be increased for saccades to novel targets, but found just the reverse effect: novelty was associated with *less* variability. We calculated the standard deviation of the angular spread of saccades directed towards each of 99 novel and 11 familiar targets from all 11 experiments. On average, saccades to familiar targets had a standard deviation of 6.6° of arc. Saccades to nearby novel targets were less variable in the majority of conditions (68 of 99, evenly distributed across monkeys and directions). The effect was even stronger when saccades to the novel targets closest to a familiar target were excluded: for saccades to novel targets 4°, 8° or 16° from a familiar location, fully 60 out of 82 (73%) were less variable (more precise) than saccades to a familiar target. Surprisingly, even saccades to near-vertical novel targets showed increased precision (in 25 of 35 conditions) when compared to saccades to near-vertical familiar targets.

The fact that novel targets were associated with less variability is consistent with the finding that saccades to novel targets have lower error rates (Table 1). As suggested earlier, novelty may cause an increase in alertness, and this may in turn lead to more precise targeting. This means that novelty may influence saccade behavior even in the absence of an effect on mean saccade endpoints.

The novelty of targets only 1° or 2° from a familiar location was apparently not recognized, or at least had no noticeable effect on behavior. Saccades to these targets were most often not repulsed from nearby familiar locations (Fig. 3), and the variability of these saccades was similar to the variability of saccades to familiar targets. In particular, half of these cases (8 out of 17) showed increased variability while half showed decreased variability.

4. Discussion

The findings presented here suggest that a saccade to a familiar location is not performed by executing an overtrained, memorized movement. In eleven experiments in five animals, it was never the case that a memory-guided saccade to a novel target was systematically deviated towards the location of a nearby fa-

miliar target. This indicates that monkeys do not merely register the approximate location of the target and then use that approximate location to select one of a small number of previously memorized target locations or saccade trajectories. Instead, a sensory to motor transformation is performed on every trial, using information gleaned on that trial.

Saccades towards novel targets located close to the vertical meridian were influenced by previously memorized target locations, however. Surprisingly, these saccades were biased away from the previously learned locations.

We will first raise and then rule out one possible objection to our principal conclusion that saccadic trajectories to familiar targets are not influenced by their familiarity. Next, we will discuss the fact that novelty, not just proximity to the vertical meridian, was an important factor in the repulsive bias observed. We will then briefly discuss how the results of this experiment relate to previous studies. Finally, we will ask whether our conclusions can be applied to situations that extend beyond the specifics of our paradigm.

4.1. Saccades to familiar targets do not make use of stored trajectories

If memory-guided saccades to familiar targets or locations rely on stored representations of trajectories or movement endpoints obtained from previous trials, then saccades to novel targets close to these familiar targets should be influenced by positions of familiar targets. We saw no evidence of such bias for familiar targets away from the vertical meridian, and therefore conclude that memory-guided saccades to familiar targets are directed only by spatial information obtained on the current trial, and do not utilize stored representations of trajectories or locations from past history.

However, a logical objection can be raised. Saccades to novel targets showed increased precision, decreased error rate, and (for saccades near familiar vertical targets) repulsion away from nearby familiar target locations. Thus, novel targets are treated differently from non-novel targets. Given this fact, it may be incorrect to use a property of novel saccades (in particular, the absence of a bias towards nearby familiar locations) to draw a conclusion about familiar saccades (in particular, that they do not rely on previous knowledge regarding the location of the familiar target).

This argument can be addressed in the following manner. The novelty of targets within 1° or 2° from a familiar location is apparently not registered by the system. First, saccades to such targets do not show the repulsion effect displayed by more eccentric novel targets. Second, saccades to these targets do not show the reduction in variability seen for saccades to more eccentric novel targets. Yet even saccades to targets close to a familiar location show no evidence of bias towards that familiar location, neither in the case of near-vertical targets (Fig. 3) nor in the case of targets far from the vertical meridian (data not shown).

To summarize, saccades to novel targets lying very near to familiar locations are not singled out, and yet there is no evidence that these saccades are biased towards the familiar target location. Therefore, it appears likely that saccades to familiar target locations far from the vertical meridian are guided based solely on the visual spatial information obtained on that particular trial, with minimal reliance on information obtained on previous trials.

4.2. Repulsion depends on both target novelty and proximity to the vertical meridian

In the first three animals tested, three of the five familiar targets were located on the horizontal or vertical meridians. Saccades directed towards novel targets near the vertical meridian were repulsed away from the vertical meridian. This repulsion could have been entirely unrelated to the previous training history of the animal, and instead related only to the vertical nature of the saccade. To test this idea, we trained two additional animals using a familiar target 8° off the vertical meridian. Two findings from these animals show conclusively that the repulsive bias depended on target novelty. First, saccades towards the familiar target just off the vertical meridian were not deviated away from the meridian, showing that saccades are not always deviated away from vertical. Second, saccades to novel targets located between the familiar target and the vertical meridian were deviated away from the familiar location, that is, towards the vertical meridian rather than away from it. These results show that the bias we observed was not due to the absolute target direction per se, but instead reflects an interaction between novelty and absolute location.

Why should the bias occur only near the vertical meridian? Both neurophysiological and psychophysical studies have revealed ways in which the vertical meridian is privileged. In many visual and oculomotor areas of the brain, the neural representation of the vertical but not the horizontal meridian is discontinuous (e.g., V1 (Daniel & Whitteridge, 1961), and superior colliculus (Robinson, 1972)). Cells in V1 prefer vertical and horizontal orientations to oblique orientations (Mansfield, 1974). Allocating attention to the right or left hemifield results in a contralateral deviation of saccades to targets along the vertical meridian (Sheliga, Riggio, Craighero, & Rizzolatti, 1995). In perceptual tasks, horizontal and vertical orientations are more easily identified than oblique orientations (Appelle, 1972; Howard, 1982; Sekular & Blake, 1994). Interestingly, however, we did not observe the repulsion effect with targets close to the

horizontal meridian, but only with those close to the vertical meridian (Table 2).

Could it be that targets close to the vertical meridian are easier to classify as either novel or familiar? If a novel location far from the meridian cannot be distinguished from a nearby familiar location, then the nearby familiar location can hardly act to bias the saccade to the familiar location. However, there were clear behavioral differences in the error rates and precision of saccades to novel and familiar targets, and these behavioral differences were independent of distance from the meridian. Therefore there is no evidence to support the idea that the familiarity or novelty of a target close to the vertical meridian was easier to detect than the familiarity or novelty of a target far from the vertical meridian. Thus, the two effects of novelty—biasing away from familiar target locations, and increased precision—may arise from two different mechanisms.

4.3. Relationship to previous work

Our finding that saccades are biased away from familiar locations is reminiscent of similar findings in research on humans showing that spatial memories are biased away from perceived boundaries (Gourtzelidis et al., 2001; Huttenlocher et al., 1991; Sandberg et al., 1996). In these paradigms, subjects used arm movements to indicate the location of a remembered target. Reported locations were biased away from imaginary vertical and horizontal meridians through the space in which subjects could respond. A model proposed by Huttenlocher et al. (1991) suggests that subjects perceive these horizontal and vertical meridians as category boundaries and categorize targets as being on one or the other side of these boundaries. According to this model, the bias occurs because the target location is coded in part in terms of its relationship to the boundary. Therefore errors, when they occur, tend to be toward the prototypical value of that category: away from the boundary.

Perhaps this implies that in our paradigm, the vertical meridian itself acts as an exact boundary. This idea is ruled out by the 8° off-vertical experiments in monkeys J and H. It is possible, however that there is an imprecise boundary between left and right which can be captured by a frequently presented target.

Interestingly, Sandberg et al. (1996) found that these biases do not occur as strongly in young children who may have less experience with remembering locations with respect to boundaries than older children and adults. Similarly, when monkey J was less experienced with the familiar target locations there was a trend for his repulsion bias to be smaller than when he had more experience. This is further evidence that the familiarity of a target, not just its location, is important in producing the repulsion effect.

4.4. Generalizability of these findings

Our data were obtained under a very limited set of circumstances. Perhaps the most severe limitation is that we do not know whether distortions occurred in perceptual processing, in sensory to motor transformations, in saccade execution, or during information storage. These issues could be partially addressed by varying the memory period duration or by requiring output using other effector systems (e.g., reaching or making perceptual judgments while maintaining fixation). There was some suggestion that effects were stronger with longer memory periods, but in our data longer memory periods were correlated with longer training prior to testing, thereby confounding the results. Clearly, experiments addressing this issue are indicated, although we suspect that their interpretation, like the interpretation of many analogous data sets, will not be straightforward.

Our data were collected using macaque monkeys. It is unclear whether these results will transfer to other species, most notably human. However, the data cited on biases induced by boundaries were obtained in humans (Huttenlocher et al., 1991), and other spatially-specific distortions of saccades to remembered locations have been identified in both humans and monkeys (Gnadt, Bracewell, & Andersen, 1991), so we think it likely that similar effects will be seen in humans.

In this study we considered only the direction of saccades. In preliminary studies we considered saccadic amplitude. We found that, even with visually-guided saccades, saccade amplitudes were subject to strong range effects (Kapoula, 1985). In our memory-guided saccade tasks, we found that these range effects were very large, and would have completely obscured any novelty effects that might have existed (unpublished observations). Range effects were minimal in the current study, and in any case cannot explain repulsion of saccades away from targets close to the vertical meridian, which lay in the very center of the range.

In conclusion, we have shown that monkeys plan saccades towards familiar locations using precise spatial information from the current trial, and are not biased towards representations which might have been learned over the course of previous trials. Despite this, there were two effects of saccades to novel targets. First, saccades to novel targets were more precise than saccades to familiar targets, which may reflect non-specific alerting as a consequence of seeing an unusual stimulus. Second, novel saccades close to the vertical meridian were biased away from previously learned familiar locations. Thus, although familiar saccades were not affected by previously overtrained target representations, such contamination did occur for novel saccades around a familiar near-vertical target.

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